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# Role of Microorganisms in Alleviating Abiotic Stresses

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## Abstract

Constantly changing agroclimatic scenario has raised serious threats to agricultural production and productivity nowadays. Current attempts toward attenuation of abiotic stressor(s) have met limited success. Among the several strategies proposed, microbial mitigation of abiotic stresses has gained rapid attention, particularly in light of its sustainable and green approach that utilizes the natural phenomenon of plant-microbe association and subsequent beneficial interactions. The role of phyllosphere, rhizosphere, and endophytic microorganisms in mitigating a variety of abiotic stressors is well known. However, limited information is available till date regarding the cumulative influence of abiotic stressor(s) on plant-microbe association and on the stress-mitigation potential of microorganisms as well. Microbial inoculation is frequently recommended under stress-prone environment; however, it appears quite crucial to understand the behavior of inoculants under stressed habitats, which could substantially reduce the failure encountered by microbial inocula. This chapter typically highlights the plant-microbial interactions under abiotic stresses, microbial adaptations, and the role of stress-resilient microbes in alleviating the same.

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## Keywords

Abiotic stress · Microbial community · Phyllosphere · Signaling · Biomolecules · Secondary metabolites

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## 6.1 Introduction

Plants meet a variety of abiotic factors under constantly changing environmental conditions. Most of the extreme abiotic factors are detrimental to plants, which significantly influence the growth, development, and productivity. All such abiotic factors are cumulatively termed as abiotic stresses. Prominent abiotic stressors include salinity, drought, low/high light, heavy metals, acidity, sodicity, wind, heat, frost, flood (submergence), etc. (Wang et al. 2003; Agarwal and Grover 2006; Nakashima and Yamaguchi-Shinozaki 2006; Bailey-Serres and Voesenek 2008). Exposure of a stressor or a combination thereof may be either acute or chronic in nature. The influence of plant growth, however, depends on the intensity of the stressor, duration of the stressor, growth stage and physiology of the plant, and ultimately the susceptibility of the cultivar.

Plants execute intrinsic combat mechanisms to restrict the adverse influence of various stressor(s). These mechanisms include avoidance, early senescence, development of resistance, expressions of different heat shock proteins (HSPs), antioxidant enzymes, accumulation of osmolytes, etc. (Scarpeci et al. 2008; Atkinson et al. 2013; Prash and Sonnewald 2013). However, these mechanisms often are overcome by the stressor, making the adverse influence visible in terms of retarded growth, development, and productivity of the plant.

The additive effect of plants' intrinsic stress-combat mechanisms has been observed in the presence of plant growth-promoting (PGP) microorganisms. Many PGP microbes have been shown to actively induce the synthesis and increase in the levels of antioxidant enzymes, accumulation of osmolytes, and expression of different stress-responsive genes. The ability of microbes to enhance germination and establishment of juvenile seedlings under the influence of different abiotic stressors is well known. A variety of PGP bacteria, fungi, and actinomycetes, either individually or in the consortium form, have been demonstrated for their plant-beneficial interactions with abiotically stressed environments (Braud et al. 2009; Hayat et al. 2010; Baltruschat et al. 2008; Wang et al. 2012). Besides executing direct interaction with the plant, the microbes also enhance sustenance of the plant under stress conditions by altering soil properties, e.g., mycorrhiza and other plant-beneficial fungi form a network of hyphae in root proximity, which promotes soil aggregation and thus the colonization (Calvet et al. 2004). This chapter typically covers the beneficial interactions between plant and the associated microflora under abiotically stressed habitats and the role of plant-associated microbes in mitigation of different abiotic stresses.

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## 6.2 Plant-Microbe Interactions Under Abiotic Stress

Both the plant growth, development, and productivity and native microbial population from the soil are negatively influenced following exposure to abiotic stresses. The microbes being prokaryotic entities suffer drastically. However, a chronic exposure of the stressor can potentially induce adaptations in microbes to the altered environmental conditions. It is thus a fraction of soil flora managed to sustain under abiotic stress.

Besides availability of the soil microflora, plants suffering from abiotic stress fail to project colonizing signals in the form of root exudations (which gets altered following exposure to stress), thus leading to decreased colonization (Kamilova et al. 2006). This cumulatively influences the growth and development of the plant and worsens the adverse effects of the stressor.

### 6.2.1 Influence of Stress on Plants

Plants generally encounter a combination of abiotic stressors under in situ conditions. The influence of any number of stresses at a given point of time varies drastically with the determinant factors such as duration of exposure, growth stage, susceptibility, etc. Moreover, many times a combination of stresses helps reduce the adverse effects of each other (Iyer et al. 2013). Influence of temperature stress on an antioxidative defense system of wheat seedlings may be altered by water/salt stress in wheat seedlings (Keles and Oncel 2002). Mitigation of plants to a combination of drought and heat stress cytosolic APX1 plays a central role (Koussevitzky et al. 2008). Plants exposed to drought, heat stress or a combination of drought and heat stress have been shown to accrue sucrose other sugars such as maltose and glucose (Rizhsky et al. 2004).

At earlier stages, e.g., germination, abiotic stresses like drought, salinity, exposure of heavy metals, and acidic/sodic conditions exert prominent influence on seed germination that declines severalfold (McCue and Hanson 1990; Keles and Oncel 2002). Moreover, the seeds that managed to germinate successfully often show reduced vigor and thus exhibit poor establishment, which ultimately hinders the subsequent development of the plant and thus the productivity. Further, the plants suffering from abiotic stresses show altered root exudation, which hampers the rhizosphere signaling cascades that play crucial role in microbial colonization. Lack of important nodes in signaling cascades significantly reduces the microbial colonization, which further weakens the plants' combat mechanisms against the stress situation. Decreased resistance to the stressor significantly retards the growth and development of the plant, which ultimately result in declined yield.

### 6.2.2 Influence of Stress on Microbes and Microbial Colonization

As discussed earlier, microbes are relatively more susceptible to adverse conditions. They undergo rapid metabolic and physicochemical changes following the exposure to abiotic stress. This directly affects the qualitative and quantitative metabolism of the microorganisms from the stressed environment. Moreover, such stress-driven metabolic hindrances in microbes ultimately influence the important nodes of rhizosphere signaling cascades (Sadowasky 2005) and also the abundance of plant-beneficial biomolecules of microbial origin in the phyllosphere environment.

Another important factor to be considered while considering the influence of abiotic stress on microbes is the resilience of the native microbial community. The lesser the resilience of a microbial community to abiotic stressor(s), the lesser the chances of survival following the exposure. However, a chronic exposure to abiotic stressor(s) can induce adaptive changes in a fraction of native microbial population, which efficiently manage to perform routine metabolic reactions even under the influence of the stressor(s) (Meena et al. 2017). Thus sudden onset of stressor(s) can impose peak damage to microbial richness of the habitat, while a chronic exposure may potentially induce resilience among the candidate members of native microbial community. Abiotic stressors such as salinity, prolonged drought, acidity, sodicity, etc. often are chronic in nature; the habitats suffering from similar circumstances can potentially provide a plethora of adapted PGP microbial strains, which could probably be utilized as inoculants for alleviation of the particular stressor(s) at different sites (Omar et al. 2009; Tiwari et al. 2011; Sorty et al. 2016).

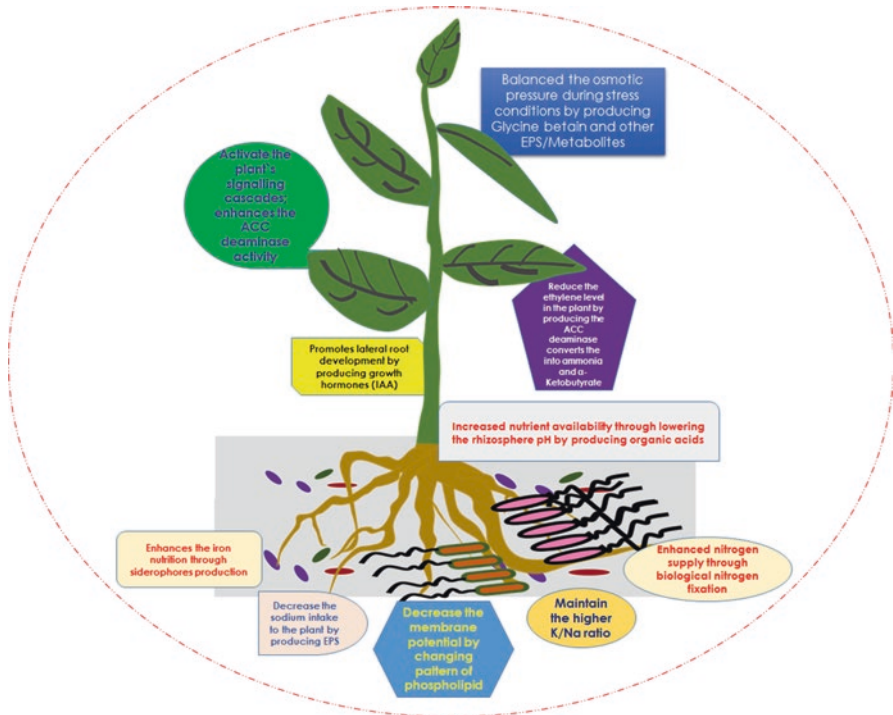
### 6.2.3 Interactive Effect of Stress on Microbial Colonization

Microbes colonize the phyllosphere by responding to different signals projected by plants. The colonizing microbes themselves also are known to communicate by projecting an array of signaling molecules that predominantly include microbial secondary metabolites. Stress-governed metabolic hindrance in microbes may potentially deviate the metabolic pathways and alter/completely cease the production of important metabolite mediators in signaling cascades (Paul 2012).

Similarly, the plants also suffer in terms of stress-induced metabolic hindrances, which affect the metabolic fluxes and thus the quality and quantity of root exudations, which fail to attract the microbes from the surrounding environment. Rhizosphere microorganisms, mainly beneficial bacteria and fungi, can enhance plant growth under stress environments and, consequently, enhance yield (Dimkpa et al. 2009), (Fig. 6.1). Absence of beneficial microbes in the phyllosphere region exerts negative influence on plants' growth and overall development. Thus ensuring optimum colonization under stress conditions represents an important task. Many observations have demonstrated the negative influence of abiotic stress conditions on microbial colonization in phyllosphere region. Under drought conditions, nodule initiation, formation, and development and nitrogen fixation are inhibited by lower water content (Serraj 2003); it inhibits nodule oxygen permeability and nitrogenase activity (Serraj and Sinclair 1996).

### 6.2.4 Microbes Mediated Alleviation of Abiotic Stress

Microbes carry out a variety of metabolic operations in phyllosphere region, which influence plant growth. Different biomolecules are produced by microbes that potentially act as plant growth regulators. Under stress-prone conditions, such molecules play vital role in plants' tolerance to the adverse circumstances. Most



**Fig. 6.1** The figure illustrates the mechanisms involved in microbe-mediated abiotic stress tolerance in crop plants. The application of nonpathogenic, plant growth-promoting bio-inoculants plays varying roles in the root zone or rhizosphere and enhances the stress tolerance. The presence of plant growth-promoting bacteria in the root zone alters the selectivity of the ions like  $\text{Na}^+$ ,  $\text{Ca}^{++}$ , and  $\text{K}^+$ , thus enabling the plant to maintain higher  $\text{K}^+/\text{Na}^+$  ratio. The members of PGP bio-inoculants make changes in components of the membrane particularly in phospholipids which ultimately alter the saturation patterns and reduce the membrane potential. Plant growth-promoting bacteria promote the lateral root development by producing the growth hormones like IAA which ultimately increases the total root surface area and enhances the plant tolerance toward different stressors. Bacteria help the plant accelerate the osmotic adjustment by producing variety of osmolytes like glycine, betaine, etc. Bio-inoculants activate the signaling cascades which help the host plant to maintain its defensive physiological state and also reduce the ethylene levels in the plant with the help of ACC deaminase. Bio-inoculants also enhance the nitrogen availability and other nutrients' availability through biological nitrogen fixation and lower the rhizosphere pH by producing the organic acids. Microorganisms also provide the fitness to the plants under abiotically stressed conditions by increasing the iron nutrition by producing siderophores. Further, microbes also reduce heavy metal toxicity by reducing their availability to the plants via production of diverse kinds of exopolysaccharides (EPS) and also through binding of the elements in biologically unavailable form

predominant molecules include microbial derivatives of plant growth hormones (PGHs), enzymes like ACC deaminase, siderophores, microbial exopolysaccharides (EPS), etc. (Fig. 6.1). All such direct and indirect biomolecular interactions between the associated microbes and plants are cumulatively studied under beneficial microbe-plant interactions under stress.

#### 6.2.4.1 ACC Deaminase Production

Plant growth-promoting bacteria are able to produce ACC deaminase to lower plant ethylene level (Fig. 6.1). Ethylene is synthesized in higher plants, under a variety of abiotic as well as biotic stresses. Ethylene is a key modulator in the development and growth of the plant. Ethylene can affect all stages of plant development such as plant tissues like roots, stems, leaves, flowers, and fruits. Under abiotic stress conditions, the level of ethylene in higher plant is increased. ACC deaminase producing microbial strains facilitate plant growth, by lowering the levels of ethylene (Saleem et al. 2007). This enzyme is responsible for the cleavage of the plant ethylene precursor – 1-aminocyclopropane (ACC). Rhizobial strains that are able to produce ACC deaminase enzymes are 40% more efficient in producing nitrogen-fixing nodules than other strains that do not have this trait (Ma et al. 2003a, b). Production of ACC deaminase by plant growth-promoting bacterial strains also stimulates growth of plants in biotic stress that also provide protection to the plant by ethylene causing damage resulting in infection by a pathogen. Transgenic tomato (*Lycopersicon esculentum*) plants expressing the *acdS* gene from *Enterobacter cloacae* UW4 were distinctly positioned under the transcriptional control of 35S CaMV, rolD promoter, and *prb-1b* promoter that have been considered for their reaction due to submerging stress (Grichko and Glick 2001a, b). The transgenic canola plants were also developed expressing *acdS* gene from *Pseudomonas putida* UW4 under the control of root-specific rolD promoter from *Agrobacterium rhizogenes* to evaluate their response toward submergence tolerance (Farwell et al. 2007). Pea (*Pisum sativum* L.) seeds, coated with rhizobacterial strains capable of producing ACC deaminase, successfully eliminated the influence of drought stress on growth and ripening (Arshad et al. 2008). Soil inoculation with a natural root-associated bacterium *Variovorax paradoxus* 5C-2 was found effective in enhancing the yield of pea (*Pisum sativum*) plants grown in drying soil conditions (Belimov et al. 2009). Rhizobacteria isolated from rice rhizosphere containing ACC deaminase were also found effective in enhancing salt tolerance and consequently improving the growth and development of rice plants under salt-stress conditions (Bal et al. 2013).

#### 6.2.4.2 Microbial Volatile Organic Compounds (MVOCs)

Microbial volatile organic compounds (MVOCs) are synthesized by numerous microorganisms ranging from bacteria to fungi. MVOCs have prospective as promising replacements to harmful insecticides, fungicides, and bactericides as well as genetic modification. MVOCs are complex mixture of low molecular weight compound and are vital infochemicals mediating essential communication systems in all kingdoms of life (Hare 2011; Dweck et al. 2015; Bitla et al. 2017). MVOCs are involved in plant rhizospheric processes like competence, pathogenesis, and symbiosis and also work as quorum-sensing signal molecules for both microbial growth and root development (Ortiz-Castro et al. 2008, 2011; Chernin et al. 2011). Rhizospheric bacterial strains release several VOCs that can potentially control both the plant growth promotion and root-system development (Gutierrez-Luna et al. 2010); some studies have demonstrated that PGPR volatile emission triggers the ISR in plants to tolerate abiotic stresses like salinity and drought (Yang et al. 2009). *Bacillus subtilis* strain GB03 and

*Bacillus amyloliquefaciens* strain IN937a emitted volatiles that considerably decrease the severity of disease on *Arabidopsis thaliana* affected by *Pectobacterium carotovorum* subsp. *carotovorum* and promote the growth of the plant (Ryu et al. 2003, 2004). *Fusarium oxysporum* MSA 35 produces VOC  $\beta$ -caryophyllene which induces shoot length, root length, and fresh weight of lettuce seedlings (Minerdi et al. 2011). 2R,3R-butanediol volatile compound produced by a *Pseudomonas chlororaphis* O6 is responsible for the development of induced systemic resistance *Arabidopsis thaliana* against drought (Cho et al. 2008). Rhizobacterial strain *B. subtilis* GB03 VOC emission controls the auxin production and cell development in *Arabidopsis thaliana* (Zhang et al. 2007). Roots of *A. thaliana* seedlings were inoculated with a suspension of *Bacillus subtilis*; acetoin emitted by *B. subtilis* triggers the ISR (Rudrappa et al. 2010). More than over 1000 microbial volatiles are described and documented in a distinct database for microbial VOCs called mVOC<sup>1</sup> (Lemfack et al. 2014). The numbers of volatiles reported are very low as compared to the microbial diversity present in soil; there is need of more study about MVOCs for application in agriculture against the abiotic stress.

#### 6.2.4.3 Production of Microbial Derivatives of Plant Growth Hormones (PGHs)

Plant growth hormones synthesized by microbes are well studied. Hormones like auxins and cytokinins are known to play key role in the plant-microbe signaling as well as regulation of the plants' growth (Meena et al. 2012). Auxins and cytokinesis are also involved in the regulation of the symbiotic nitrogen fixation of rhizobium-plant interaction (Allen et al. 1953). The influence of cytokinins in the initiation of nodule organogenesis was also well studied in diverse legumes, where exogenous applications of cytokinins successfully induced amyloplast accumulation, cortical cell divisions, and the expression of initial nodulation indicators (Torrey 1961; Dehio and deBruijn 1992; Mathesius et al. 2000; Murray et al. 2007). Indole-3-acetic acid (IAA) is the most widely studied plant hormone – a carboxylic acid having a carboxyl group linked with a methylene group to the 3rd carbon of the indole ring (Thimann 1939). Commonly majority of the auxin-producing bacteria produce IAA, while some of the other bacteria produce GA3 and other derivatives. IAA also has the ability to influence the gene expression in microbes; thus IAA contributes central role in plant-microbe interaction (Fig. 6.1). Moreover, it is also involved in the adaptation of plant to abiotic stresses like salinity and drought (Spaepen and Vanderleyden 2011). IAA and GA3 induce the growth and are also involved in the development of plants' root system (Atzorn et al. 1988; Bottini et al. 2004). A recent study demonstrated that *Pseudomonas* sp., *Rhizobium* sp., *Enterobacter* sp., *Pantoea* sp., *Marinobacterium* sp., *Acinetobacter* sp., and *Sinorhizobium* sp., able to produce IAA, have significant influence on germination and seedling growth in wheat under saline condition. *Pseudomonas* sp. and *Acinetobacter* sp. were also described to enhance production of IAA in barley and oats, in salinity stress conditions (Chang et al. 2014). Cytokinins producing bacterial strains can also enhance the growth under drought stress (Arkhipova et al. 2007)

#### 6.2.4.4 Nutrient Cycling

The plant depends on bioavailability of both macro- and micronutrients. Most of the times, abiotic stress situation alters the soil properties; for instance, conditions like salinity, acidity, alkalinity, metals contamination, etc. induce drastic changes in the physicochemical properties of soil. This badly affects the bioavailability of nutrients from the soil. The altered soil pH can potentially induce chemical changes among soil nutrients, thereby making them biologically unavailable. Such nutrients though are available in the soil, they become biologically unavailable, to which plants fail to absorb, which directly influence the plant growth. For instance, a change in pH toward the alkaline side drastically affects the  $\text{Fe}^{2+}$  content from soil, which gets converted into  $\text{Fe}^{3+}$ , for uptake of which a strong chelating system is required, which constitutes a class of molecules called siderophores (Fig. 6.1). Though some monocots have been shown to produce siderophores, the iron supplemented by them appears insufficient for the plant. Under such circumstances, microbial siderophores can contribute significant role in Fe fulfillment to the plant (Kumar et al. 2008). The rhizosphere microbes produce relatively large quantities of siderophores which actively chelate  $\text{Fe}^{3+}$  and facilitate its bioavailability. Many siderophore-producing microbes have been shown to actively enhance iron fulfillment to the plant under iron-starved soils (Hao et al. 2012; Supanekar et al. 2013). Similarly, the bioavailability of other micronutrients is also known to facilitate the rhizosphere microbes under starved conditions.

Fixation of atmospheric nitrogen by rhizosphere microbes is another important task. Many microbial strains have been described in literature for their exceptional ability to fix atmospheric nitrogen under abiotic stress environment (Bianco and Defez 2009; Casanovas et al. 2002). Legume-rhizobium symbiosis has been found to be very sensitive to water-deficit condition (Kirda et al. 1989). Indigenous strains of *B. japonicum* were working inoculant than commercial strains of rhizobium once soybean grows under drought conditions (Hunt et al. 1988). The use of such resilient nitrogen fixers under the influence of stressors like salinity and altered pH conditions can ensure a sustainable supply of nitrogen, as addition of chemical fertilizers may worsen the situation over prolonged period. AM fungus *Glomus mosseae* was shown to contribute major role in the improvement in plant dry mass, nitrogen-fixing potential of nodules, and offering protection to the olive plant from harmful impact of salinity (Porrás-Soriano et al. 2009).

Subsequently nitrogen and phosphate are the most necessary nutrients for the plant growth, but a soluble form of phosphate in soil is very low around 1 mg/kg or less (Goldstein 1994). Phosphate solubilization is another important trait of plant growth-promoting microbes. This trait is typically attributed to the organic acids produced by microbes as metabolic products (Fig. 6.1). The enzyme phytase has also been shown to have a significant role in phosphorus mobilization by microorganisms (Kohler et al. 2007). The ability of microbial strains to solubilize phosphate under abiotically stressed conditions like salinity is well known (Bianco and Defez 2010; Mishra et al. 2016); *P. oxalicum* and *P. expansum* indicated different stages of phosphate solubilization under saline stress (Hefnawy et al. 2014); bacterial strains from genera *Pseudomonas*, *Rhizobium*, and *Bacillus* and enterobacteria as well as



*Penicillium* and *Aspergillus* fungi are the most dominant P solubilizers (Whitelaw 2000). Such stress-resilient microbes demonstrate their metabolic efficiency and thus the adaptations under abiotic stress conditions. Similarly mobilization of potash is also achieved by rhizosphere microbes under stressed environment.

#### 6.2.4.5 Microbial Exopolysaccharides

Microbial exopolysaccharides (EPS) are an important class of carbohydrate polymers that have a multifaceted role in the rhizosphere. They may be either homopolymers or heteropolymers, depending on the organism synthesizing. The unique property of microbial EPS to hold water (water holding capacity) further increases their importance under water-deficit conditions, where the presence of EPS can efficiently ensure the appropriate moisture supply in rhizosphere environment (Hepper 1975; Selvakumar et al. 2012; Alami et al. 2000). Additionally, microbial EPS have many reactive sites, where varieties of elements including micronutrients are trapped, which are then released slowly in rhizosphere environment. The affinity of many EPS toward  $\text{Na}^+$  has been demonstrated in many studies; this highlights the potential use of this class of compounds in remediation of saline soils (Khan et al. 2016); further they can also potentially be applied for alleviation of salinity stress through point application.

EPS also have been shown to enhance microbial colonization by providing substratum for adherence to the microbes; this phenomenon is also helpful for the development of biofilm. Moreover microbial polysaccharides are also known to have a role in rhizosphere signaling, e.g., during nodulation, root colonization, etc. (Amellal et al. 1998). Considering the beneficial influence of microbial EPS in plant-microbe interactions, there is plenty of scope for their utilization in mitigation of abiotic stresses (Fig. 6.1). *Pseudomonas* sp. PMDzncd2003 on rice germination under salinity stress is verified; superior root colonizing ability of *Pseudomonas* sp. along with its capability to synthesize exopolysaccharides (EPS) indicates better tolerance toward salinity (Sen and Chandrasekhar 2014). *Pseudomonas putida* strain GAP-P45 mitigates drought stress in *Helianthus annuus* by producing exopolysaccharide (Sandhya et al. 2009).

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### 6.3 Future Prospectus

A plethora of microbial strains have been described for their ability to promote growth by various mechanisms under abiotically stressed environments. However, the knowledge regarding their performance under field conditions appears quite limited. This leaves an excellent opportunity for the development of efficient inocula consisting of abiotic stress-resilient microbial strains, which could sustainably help mitigate the adverse effects of abiotic stressor(s) in agricultural crop. Moreover, there is also opportunity to explore novel diversity of resilient microorganisms from the habitat chronically exposed to abiotic stresses. Similarly the wild plants thriving luxuriantly under extreme environments may also be explored for candidate microbial strains which can open the new gateways in the

area of microbial management of abiotic stress in agriculture. Similarly the current knowledge regarding microbial metabolism under the influence of abiotic stresses under field conditions is also in infancy. Detailed metabolomics account of stress-governed metabolic fluctuations in PGP microbes from rhizosphere habitat can potentially pave the way for the development of novel strategies relating to the use of microbial metabolic products for alleviation of abiotic stresses in stress-affected agricultural ecosystems.

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## 6.4 Conclusions

Plant-associated microbes contribute a vital role in the sustenance and successful combat of the plant to adverse environmental circumstances generated by abiotic stressor(s). The habitats suffering prolonged exposure to abiotic stressor(s) can potentially act as reservoirs for stress-resilient PGP microbial strains that can serve the role as efficient stress alleviators in agriculture crop, thus promoting sustainable management of abiotic stresses under changing climate scenario.

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